

Penaeid shrimps – their biology and management

**Selected papers presented at the workshop on the
scientific basis for the management of penaeid
shrimp held at Key West, Florida, U S A,
November 1981**

The workshop was sponsored by:

**U S Department of Commerce, NOAA/NMFS
Southeast Fisheries Center, Miami, Florida
Gulf States Marine Fisheries Commission, Ocean
Springs, Mississippi**

in collaboration with the

**Food and Agriculture Organization of the U N
Fishery Resources and Environmental Division,
Rome, Italy**

Edited by:

Dr John A Gulland

**Fishery Resources and Environmental Division
Food and Agriculture Organization, Rome, Italy**

and

Prof Brian J Rothschild

**Chesapeake Biological Laboratory
University of Maryland, Maryland, U S A**

Published by:

**Fishing News Books Limited
Farnham · Surrey · England**

1984

Interaction with other species

Ecological interactions between penaeid shrimp and bottomfish assemblages

*Peter F Sheridan
Joan A Browder
and Joseph E Powers*

Abstract

A biological review identifies potential ecological interactions between commercial penaeid shrimp and bottomfish that share the same habitat and are caught with shrimp in trawls, then returned to the sea as carrion. Two models are used to evaluate the possible impact on shrimp stocks of reducing the quantity of fish discarded, assuming certain ecological interactions exist. The first model, using a classical population dynamics approach, treats the problem as one of two stocks exploited by a common fishery, each partially supported by the discards of the other. Conclusions from this model are that the elimination of bottomfish discards could reduce shrimp production by only a small amount. The energy-flow ecosystem model treats the problem as one of 11 trophic compartments linked by the flow of energy and the cycling of nitrogen. In this model system, a reduction in discards through utilization of one-half the by-catch reduces shrimp stocks by 25 percent, but a reduction in discards through the use of special trawls with one-half the catch-efficiency for fish reduces shrimp stocks by only 8 percent, even in the 'worst case' of bottomfish predation on shrimp. In the model system, there is no long-term impact on shrimp of reducing discards by means of special trawls, if bottomfish are moderately selective against shrimp relative to their biomass in the environment.

Introduction

Penaeid shrimp are a highly prized seafood harvested from coastal tropical and warm-temperature waters throughout the world. Bottomfish of many species are harvested in large quantities in the shrimp trawling operation. The species composition of this by-catch varies with time and area,

but it is generally dominated by sciaenids, pomadasysids, sparids, synodontids, serranids, and bothids. Determination of the nature and extent of ecological interactions between shrimp and bottomfish is important in managing the shrimp fisheries and in exploiting the bottomfish resources.

Direct interaction can be limited to predation, competition or scavenging. Scavenging may be of significance because of the quantity of the trawl catch that is discarded. A large proportion of the bottomfish catch is discarded due to the higher value of shrimp. Some shrimp also are discarded due to size requirements, and are lost during the bottomfish culling process. In this paper we investigate the likely magnitude of shrimp/bottomfish interactions by presenting 1) an extensive review of the biological information on shrimp and bottomfish assemblages, 2) an analytical model to assess the impacts of discards, and 3) an energy flow model of the shrimp/bottomfish ecosystem that evaluates the possible effect on shrimp of reducing discards by two alternative methods. We then make some qualitative conclusions about the importance of considering interactions between shrimp and bottomfish in the management of these resources.

Biological review of shrimp/bottomfish assemblages

Distribution of major shrimp grounds and associated fishes

Penaeid shrimps support commercially valuable fisheries in many areas of the world which lie between 35° north and south of the equator (Turner, 1977). At least 97 species in the family Penaeidae are of commercial interest (Holthuis, 1980). The Food and Agriculture Organization of the United Nations publishes yearly summaries of

global fisheries statistics. The 1978 summary identifies 21 species of penaeid shrimps which contributed to overall shrimp landings of 1 474 176 metric tons (Table 1, FAO, 1979). For all shrimps, the major catch areas were Western Central Pacific, Western Indian Ocean, Western Central Atlantic, and Northwest Pacific, in order of decreasing catch. By region, the predominant shrimps were: Western Central Pacific—*Penaeus merguensis*, *Metapenaeus* spp., and *Penaeus* spp.; Western Indian Ocean—unspecified *Natantia*; Western Central Atlantic—*Penaeus aztecus*; Northwest Pacific—*P. japonicus*. Although penaeids are taken world-wide, they represent only a small portion of total fisheries production. In fact, for countries which reported penaeid shrimps specifi-

cally (rather than as 'Natantia'), penaeids comprised less than 10% of the total fisheries catch in 18 of 21 countries (Table 1). Penaeids were a significant portion of the total fishery catch only in Honduras (35.7% by weight), Guatemala (51.4%), and El Salvador (72.2%). Countries with large overall fisheries generally showed proportionally low penaeid catches; Japan, 0.1%; U S A, 3.5%; Thailand, 1.5%; Indonesia, 2.9%; Spain, 0.2%.

Very little is known concerning the bottomfish assemblages associated with shrimping grounds outside of the Gulf of Mexico. Allsopp (M. S.) estimates a weight ratio of discarded fish to shrimp in Caribbean shrimp fisheries ranging between 3:1 and 20:1. Off the Amazon River delta of Brazil,

Table 1
RECENT CATCHES OF PENAEID SHRIMPS FROM 1978 WORLD CATCH RECORDS (FAO, 1979)

Total catch of all shrimps: 1 474 176 metric tons		
Major species	Weight (mt)	Primary areas
<i>Penaeus aztecus</i>	63 624	U S A
<i>Penaeus merguensis</i>	40 098	Indonesia (70%)
<i>Penaeus duorarum</i>	25 347	U S A (65%), Cuba (20%)
<i>Penaeus monodon</i>	17 599	Indonesia (90%)
Major species and countries (both in decreasing order of abundance)		
<i>Penaeus</i> spp. (unspecified)	U S A, Philippines, Panama, Honduras, Cuba, Colombia, Costa Rica, Guatemala, Sierra Leone, El Salvador, Peru	
<i>P. aztecus</i>	U S A	
<i>P. merguensis</i>	Indonesia, Thailand, Papua-New Guinea	
<i>Metapenaeus</i> spp.	Indonesia, Thailand, Korea, Papua-New Guinea	
<i>P. duorarum</i>	U S A, Cuba, Nigeria, Spain, Gambia	
<i>P. monodon</i>	Indonesia, Thailand, Papua-New Guinea	
<i>Xiphopenaeus/Trachypenaeus</i>	El Salvador, Panama, Colombia, Guatemala	
<i>P. kerathurus</i>	Italy, Spain	
<i>P. japonicus</i>	Japan, Korea, Papua-New Guinea	
<i>P. semisulcatus</i>	Thailand	
<i>P. brevirostris</i>	Panama, Costa Rica, Guatemala, El Salvador	
<i>Sicyonia brevirostris</i>	U S A	
<i>Parapenaeus longirostris</i>	Spain, U S S R	
<i>P. chinensis</i>	Korea	
<i>Plesiopenaeus edwardianus</i>	Spain	
<i>P. californiensis</i>	Guatemala, El Salvador	
<i>Artemesia longinaris</i>	Argentina	
Major areas and species		
Western Central Pacific	<i>P. merguensis</i> , <i>Metapenaeus</i> spp., <i>Penaeus</i> spp. > <i>P. monodon</i> > <i>P. japonicus</i> , <i>P. semisulcatus</i> , <i>P. latisulcatus</i>	
Western Central Atlantic	<i>P. aztecus</i> > <i>P. duorarum</i> > <i>Xiphopenaeus</i> , <i>Trachypenaeus</i> , <i>Sicyonia</i>	
Northwest Pacific	<i>P. japonicus</i> > <i>Metapenaeus</i> spp., <i>P. chinensis</i>	
Eastern Central Pacific	<i>Xiphopenaeus</i> > <i>Penaeus</i> spp. > <i>P. brevirostris</i> > <i>P. californiensis</i>	
Eastern Indian Ocean	<i>Metapenaeus</i> spp., <i>P. merguensis</i> > <i>P. semisulcatus</i> > <i>P. monodon</i> , <i>P. latisulcatus</i>	
Southwest Atlantic	<i>Artemesia</i>	
Eastern Central Atlantic	<i>P. duorarum</i> > > > <i>P. kerathurus</i> , <i>Parapenaeus</i> , <i>Plesiopenaeus</i>	
Mediterranean/Black Sea	<i>P. kerathurus</i> > > > <i>Parapenaeus</i> , <i>Plesiopenaeus</i>	
Southeast Atlantic	<i>Parapenaeus</i> > <i>P. kerathurus</i>	

Table 1 (continued)
Penaeid catch related to total fishery catch (mt) by country

Area	Country	Species	Shrimp	Total	%
Africa	Gambia	<i>P. duorarum</i>	183	10 795	1.7
	Nigeria	<i>P. duorarum</i>	1 916	518 567	0.4
	Sierra Leone	<i>Penaeus</i> spp.	143	50 080	0.3
North Amer.	Costa Rica	<i>P. brevirostris</i>	420	14 491	7.4
		<i>Penaeus</i> spp.	189		
		Xipho/Trachy	461		
	Cuba	<i>P. duorarum</i>	5 300	213 170	3.6
		<i>Penaeus</i> spp.	2 300		
	El Salvador	Xipho/Trachy	3 849	5 487	72.2
		<i>Penaeus</i> spp.	115		
	Guatemala	Xipho/Trachy	998	3 074	51.4
		<i>Penaeus</i> spp.	583		
	Honduras	<i>Penaeus</i> spp.	2 288	6 405	35.7
	Panama	Xipho/Trachy	3 378	113 768	7.8
		<i>Penaeus</i> spp.	3 552		
	U S A	<i>P. brevirostris</i>	1 982		
		<i>P. aztecus</i>	63 624	3 511 719	3.5
		<i>Penaeus</i> spp.	35 279		
		<i>P. duorarum</i>	16 910		
		<i>X. kroyeri</i>	3 771		
South Amer.	Argentina	<i>Sicyonia</i>	1 825		
		<i>Artemesia</i>	241	537 323	0.1
		Xipho/Trachy	2 984	63 965	7.1
Asia	Indonesia	<i>Penaeus</i> spp.	1 550		
		<i>P. merguensis</i>	27 856	1 655 000	3.9
		<i>Metapenaeus</i> spp.	19 318		
	Japan	<i>P. monodon</i>	16 967		
		<i>P. japonicus</i>	3 857	10 752 163	0.1
	Korea	<i>P. japonicus</i>	3 037	2 350 778	0.3
		<i>Metapenaeus</i> spp.	2 436		
	Philippines	<i>P. chinensis</i>	1 124		
		<i>Penaeus</i> spp.	23 197	1 558 383	1.5
	Thailand	<i>Metapenaeus</i> spp.	16 707	2 264 000	1.5
		<i>P. merguensis</i>	11 685		
		<i>P. semisulcatus</i>	4 042		
		<i>P. latisulcatus</i>	1 620		
		<i>P. monodon</i>	514		
Europe	Italy	<i>P. kerathurus</i>	6 694	401 958	1.7
		<i>P. duorarum</i>	1 038	1 379 882	0.2
		<i>Parapenaeus</i>	942		
		<i>Plesiopenaeus</i>	509		
		<i>P. kerathurus</i>	17		
Oceania	Papua-New Guinea	<i>P. merguensis</i>	557	74 186	1.2
		<i>Metapenaeus</i>	213		
		<i>P. japonicus</i>	34		
	Australia	'Natantia'	18 807	122 947	15.3

Nomura and Filho (1968) found fish to shrimp ratios of 2:1 to 1:3, and the bottomfishes were primarily elasmobranchs, ariids, triglids, lutjanids, and soleids. Recent surveys by U S National Marine Fisheries Service in the same area of the Amazon delta (OREGON II cruise 84, Nov. – Dec. 1977) found lutjanids, balistids, pomacanthids, and elasmobranchs predominating offshore over hard bottoms, and sciaenids, pomadasyids, ariids, and balistids abundant inshore over soft bottoms. The average fish to shrimp weight ratio

was 9:1 at the time. Several surveys have been conducted around India. Pruter (1964) found dasyatids, sciaenids, synodontids, polynemids, lutjanids, ariids, and pomadasyids dominated the by-catch in areas where shrimp catches were small. In areas where shrimp catches were relatively large along the Indian coast, sciaenids, percids, elasmobranchs, engraulids, clupeids, and trichiurids are abundant (Muthu *et al.*, 1975).

In the Gulf of Mexico, the three dominant commercial species, *Penaeus aztecus*, *P. setiferus*, and

P. duorarum, are generally found throughout the Gulf, but each has distinctive seasons and areas of maximum abundance (Osborne *et al.*, 1969). *Penaeus aztecus* is caught primarily off the Texas and Louisiana coasts, *P. setiferus* off the Mississippi Delta area, and *P. duorarum* on the Tortugas-Sanibel grounds of Florida and the Campeche Bank area of Yucatan, Mexico. Several other genera are exploited to a lesser extent. Brusher *et al.* (1972) discussed the distributions of 9 species in the general *Sicyonia*, *Trachypenaeus*, *Xiphopenaeus*, *Parapenaeus*, and *Solenocera* on the Texas-Louisiana continental shelf. Huff and Cobb (1979) described the general ecologies of 9 species in the general *Trachypenaeus*, *Solenocera*, *Sicyonia*, *Mesopenaeus*, and *Metapenaeopsis* on the western Florida shelf.

Although the species compositions of the bot-

tomfishes found on the Gulf shrimp grounds vary somewhat with time and area, eight species (primarily sciaenids) characterize the Mississippi Delta grounds, seven species dominate in the Campeche pink shrimp grounds, and 13 species characterize the Texas and Campeche brown shrimp grounds (Table 2). A recent NMFS survey from Tampa Bay south to the Tortugas (OREGON II cruise 85, January 1978) found the six most abundant fish families to be pomadasyids, sparids, synodontids, seranids, bothids, and sciaenids.

The average ratio of fish to shrimp in shrimp catches on the Mississippi Delta grounds is approximately 14 to 1 (unpublished data, National Marine Fisheries Service, Pascagoula, Mississippi). Directed fisheries for the fish species occur in this area, most of which are harvested for pet food. Croaker (*Micropogonias undulatus*), the principal

Table 2

RELATIVE ABUNDANCES OF BOTTOMFISHES ON SHRIMP GROUNDS IN THE GULF OF MEXICO. SPECIES ARE RANKED BY RELATIVE ABUNDANCE: 1 = MOST ABUNDANT, R = RELATIVELY RARE, DASH = NOT FOUND

Brown shrimp (<i>P. aztecus</i>) grounds - Hildebrand, 1954					
Species	South Texas			Campeche	
	Nov	Jan	May	July	July-Aug
<i>Syacium gunteri</i>	1	1	2	2	4
<i>Cynoscion nothus</i>	2	R	3	5	R
<i>Cynoscion arenarius</i>	2	8	5	10	10
<i>Cyclopsetta chittendeni</i>	3	2	4	4	9
<i>Prionotus rubio</i>	4	7	R	9	6
<i>Synodus</i> spp.	5	6	6	6	3
<i>Serranus atrobranchus</i>	7	3	R	R	1
<i>Centropristis philadelphia</i>	R	4	8	R	-
<i>Stenotomus caprinus</i>	10	5	R	R	R
<i>Porichthys porosissimus</i>	R	10	R	R	2
<i>Peprilus burti</i>	R	R	1	1	R
<i>Micropogonias undulatus</i>	R	R	R	3	R
<i>Lepophidium graellsii</i>	R	R	R	R	5
Pink shrimp (<i>P. duorarum</i>) grounds					
	Campeche - Hildebrand, 1955		Tortugas		
	Feb	July			
<i>Haemulon aurolineatum</i>	1	5			?
<i>Chloroscombrus chrysurus</i>	2	2			see
<i>Eucinostomus gula</i>	3	3			text
<i>Diplectrum formosum</i>	4	6			
<i>Prionotus scitulus</i>	5	-			
<i>Stenotomus caprinus</i>	-	1			
<i>Syacium gunteri</i>	8	4			
Mississippi Delta-NMFS OREGON II Cruises 101, 10					
	White shrimp grounds		Brown shrimp grounds		
	Fall, 1979	Spring, 1980	Fall, 1979	Spring, 1980	
<i>Micropogonias undulatus</i>	1	4	1	1	
<i>Arius felis</i>	2	1	R	-	
<i>Leistomus xanthurus</i>	3	R	2	3	
<i>Cynoscion arenarius</i>	4	3	4	4	
<i>Chloroscombrus chrysurus</i>	5	R	R	-	
<i>Stenotomus caprinus</i>	R	-	3	5	
<i>Peprilus burti</i>	-	5	5	2	
<i>Cynoscion nothus</i>	R	2	R	R	

species caught incidentally in this area, are harvested for making surimi (fish paste), for a limited fresh fish market, and by recreational fisheries throughout the northern Gulf of Mexico. In the Mississippi Delta area, combined annual landings by these directed fisheries are approximately one tenth the size of the discards by the shrimp fleet.

Competitive interactions

Competition among species only occurs when a resource is in limited supply. Two basic types of competition have been recognized: 1) *interference*, in which one individual physically prevents the use of a resource by another individual either by aggression or mere physical presence, and 2) *exploitation*, in which one individual utilizes a limited resource before another individual arrives. Competition can be intraspecific or interspecific. Resources may be food, habitat, or time. Schoener (1974) has reviewed various kinds of resource partitioning, for example, species which overlap in habitat tend to have different foods, or species which have similar foods may feed at different times.

Among the penaeid shrimps and bottomfishes, sympatric species in each group often differ in their positions along such resource gradients as spawning season and depth, time or tide of migration, substrate type, temporal activity, and diet. Penaeids and bottomfishes may be in competition for certain resources when their life history stages overlap. At present, there have been no definitive explorations into potentially competitive interactions between fishes and shrimps beyond artificial laboratory studies.

Predatory interactions

All available evidence points to omnivory by penaeid shrimps, which consume varying proportions of sediment, detritus, algae, and benthic organisms. The bottomfishes, however, represent a diverse assemblage of trophic types ranging from herbivores through carnivores. The predatory interactions between penaeids and bottomfishes are basically limited to fish attacking shrimp. There are no published accounts of the reverse, but since shrimp are omnivores they are likely to feed on disabled, dying or dead fishes (eg, discarded bycatch). The impact of discarding will be discussed later in this paper. A question not yet satisfactorily answered is to what extent shrimp stocks are affected by bottomfish predation upon them.

Quantitative assessments of fish predation on penaeid shrimps are limited, and problems inher-

ent in gut contents analyses are many. Yanez-Arancibia *et al* (1976) studied the feeding of *Galeichthys* (= *Auratus*) *caerulescens* in western Mexico estuaries and found this catfish preyed mainly upon fishes and crabs. Shrimp identified as *Penaeus* spp. averaged only 7% by volume of the stomach contents and were only found in certain seasons. Bell *et al* (1978) studied the foods of an Australian scorpaenid (*Centropogon australis*) in seagrass meadow and found only a 4.3% frequency occurrence of *Penaeus* in fish stomachs, yet penaeids in that region prefer seagrass habitats over bare substrates. In Japanese estuaries, the penaeids most often eaten by fish predators are the small, non-commercial species whereas the larger commercial shrimps do not figure to any great extent in fish diets (Kakuda and Matsumoto, 1978; Kosaka, 1977, 1978).

A great deal of qualitative and quantitative information has been gathered in Gulf of Mexico studies, but it is primarily derived from estuarine investigations and rarely are prey shrimps identified beyond the categories 'shrimps' or 'penaeids'. Qualitatively, of the 42 fish species listed in Table 3, only 11 species have a 40% or greater frequency of occurrence of 'penaeids' (not just *Penaeus*) in their diets. Unfortunately, frequency of occurrence does little to quantify the importance of any food item in any diet. When some form of quantitative assessment was made (Table 4), only 8 (and probably only 4) of the 26 species examined made 'penaeids' 40% or more (by volume or weight) of their diets. In one synoptic quantitative study wherein prey shrimps were identified beyond the category of 'penaeids' in offshore fishes (Table 5), only shrimps of the genera *Sicyonia*, *Solenocera*, *Parapenaeus*, and *Trachypenaeus* were found. The genus *Penaeus* was not detected in the diets of 26 abundant offshore fishes, even though *Penaeus* inhabited the same waters. Recent studies of trawl-susceptible fishes in offshore Gulf waters (Divita *et al*, 1983; Sheridan and Trimm, 1983; NMFS, Galveston, TX, unpubl. data) found migrating juvenile and subadult *Penaeus* in less than 1% of the fish stomachs examined.

Information concerning large potential predators of both penaeids and bottomfishes is quite limited. Tunas (*Tunnus*, *Euthunnus*, *Katsuwonus*) are mainly piscivorous (Table 4). Mackerels (*Scomberomorus*), cobia (*Rachycentron*), and bluefish (*Pomatomus*) feed to some extent on penaeids as well as fishes. Sharks may also be penaeid predators but seem to prefer bottomfishes (Bass *et al*, 1973). Of the 16 species of *Carcharhinus* examined

Table 3

QUALITATIVE ANALYSES OF FISH PREDATION ON PENAEID SHRIMPS
BASED ON INSHORE (I) AND OFFSHORE (O) STUDIES

Fish predators	Percent Frequency of Occurrence				
	0	1-20	21-40	41-60	61-100
Anchoa hepsetus	I				
Anchoa mitchilli	I				
Harengula jaguana	I				
Caulolatilus chrysops	I				
Menticirrhus littoralis	I				
Katsuwonus pelamis	O				
Larimus fasciatus	I				
Thunnus thynnus	O				
Thrichiurus lepturus	I				
Raja spp.	O				
Paralichthys albigutta	I	I			
Synodus foetens	I	I			
Leistomus xanthurus	I	I			
Stellifer lanceolatus	I	I			
Thunnus albacares	O	O			
Caranx hippos		I			
Caulolatilus microps		I			
Euthynnus alletteratus		O			
Porichthys porosissimus		I			
Prionotus tribulus		I			
Stenotomus caprinus		O			
Thunnus alalunga		O			
Cynoscion arenarius		I	I		
Bairdiella chrysoura		I	I		
Urophycis floridanus		I	I		
Micropogonias undulatus	I	I, O	I		
Menticirrhus americanus	I	I	I		
Paralichthys lethostigma		I	I	I	
Lutjanus campechanus			I		
Prionotus scitulus			I		
Scomberomorus maculatus			I		
Carcharhinus sp.			I		
Rachycentron canadum				I	
Menticirrhus sp.				I	
Scomberomorus cavalla		I		I	
Arius felis	I	I		I	I
Bagre marinus		I		I	
Centropristis melana					I
Cynoscion nebulosus					I
Pomatomus saltatrix					I
Oligoplites saurus					I
Diplectrum formosum					I

See references section to specific literature

off South Africa (which has 5 species of commercial penaeids, Joubert and Davies, 1966), only 5 species fed on *Penaeus* and only to a minor extent (average, 5% frequency of occurrence).

The biological review suggests that man may be the major predator of penaeid shrimps. The consequences of interactions of man and bottomfish with penaeid shrimp will be explored in the following sections by means of a population dynamics model and an energy flow model based upon the biological review.

Both models evaluate the potential influence of

Table 4

QUANTITATIVE ANALYSES OF FISH PREDATION ON PENAEID SHRIMPS
BASED ON INSHORE (I) AND OFFSHORE (O) STUDIES. ? = PENAEIDS
NOT DIFFERENTIATED FROM OTHER SHRIMPS

Fish Predators	Percent by volume, weight or number				
	0	1-20	21-40	41-60	61-100
Anchoa mitchilli	I				
Harengula jaguana	I				
Opisthonema oglinum	I				
Leiostomus xanthurus	I				
Rhomboplites aurorubens	I				
Trachinotus carolinus	I				
Bellator militaris	O				
Prionotus salmonicolor	O				
Saurida brasiliensis	O				
Paralichthys lethostigma	I	I			
Cynoscion arenarius	I	I			
Micropogonias undulatus	I	I			
Bairdiella chrysoura	I	I			
Arius felis	I	I			
Anchoa hepsetus	O	I?			
Synodus foetens		I?			
Prionotus roseus		O			
Prionotus scitulus		I, O			
Prionotus tribulus		O			
Prionotus alatus		O			
Lutjanus campechanus		I	I		
Ancyclopsetta quadrocellata	I	I		I	
Citharichthys spilopterus		I			I
Oligoplites saurus		I?			I?
Trachinotus falcatus		I?		I?	
Haemulon plumieri		I?		I?	
Orthopristis chrysoptera			I?	I?	I?
Prionotus ophryas					O
Caranx hippos					I

See references section for specific literature

bottomfish discards on shrimp stocks, assuming certain interactions between the two stocks exist.

Impacts of interactions

In this section we will investigate analytically the impact of discarding of both shrimp and bottomfish and other interactions on the production of these populations. The analysis is meant to be illustrative in that relative changes rather than absolute values are of concern; nevertheless, some care was taken to parameterize the hypothetical models so that differences between the populations would be meaningful.

Discard model

Let us assume that the shrimp and bottomfish can be characterized as two discrete stocks which have population biomasses of P_1 and P_2 , respectively and which are exploited by a common fishery. Assume their dynamics are depicted by a simple population growth model which expresses the

Table 5
RESULTS OF A QUANTITATIVE STUDY OF FISH FEEDING ON THE GULF OF MEXICO CONTINENTAL SHELF (ROGERS, 1977). SIZE = SIZE OF FISHES. % VOL = PERCENTAGE OF VOLUME OF FISH STOMACH CONTENTS ATTRIBUTED TO SHRIMP. A TOTAL OF 4 550 STOMACHS WERE EXAMINED

Species	Size (mm : SL)	% Vol	Dominant shrimps
Anchoa hepsetus	26-125	0	
Saurida brasiliensis	51-125	0	
Halieutichthys aculeatus	26-75	0	
Ogcocephalus parvus	51-125	0	
Chloroscombrus chrysurus	101-150	0	
Stenotomus caprinus	26-125	0	
Micropogonias undulatus	51-125	0	
Bollmannia communis	26-75	0	
Peprilus burti	26-75	0	
Prionotus stearnsi	26-100	0	
Etropus crossotus	26-125	0	
Symphurus civittatus	51-150	0	
Symphurus plagiusa	101-125	0	
Synodus foetens	50-200	3	Sicyonia
Porichthys porosissimus	26-100	8	Sicyonia, Parapenaeus
Cynoscion arenarius	26-100	15	Trachypenaeus
Trichopsetta ventralis	76-125	18	Trachypenaeus, Parapenaeus
Cynoscion nothus	26-175	19	Sergestids, Trachypenaeus
Centropristis philadelphia	26-225	23	Sicyonia, Sergestids
Syacium gunteri	51-150	29	Trachypenaeus, Carideans
Prionotus rubio	26-175	29-50	Trachypenaeus, Sicyonia
Diplectrum bivittatum	26-125	48	Trachypenaeus, Solenocera
Serranus atrobranchus	26-125	49	Trachypenaeus, Sicyonia
Lepophidium graellsii	101-225	54	Carideans
Cynoscion nebulosus	26-75	57	Trachypenaeus, Sergestids
Citharichthys spilopterus	51-125	62	Trachypenaeus

change in P_i as the production minus harvest plus reassimilation if discards of P_i plus reassimilation of discards of P_j . In more mathematical terms this can be expressed as a modification to the logistic growth model

$$dP_i/dt = (a_i P_i - b_i P_i^2) - q_i f P_i + P_i(c_{ji} d_i q_i f P_j)(P_i(c_{ji} d_j q_j f P_j)) \quad (1)$$

where f = fishing effort; q_i = catchability coefficient for stock i ; a_i, b_i = production parameters for stock i ; d_i = proportion of catch of stock i which is discarded; and c_{ji} = rate of biological conversion of biomass of discards of stock j to biomass of stock i per unit biomass of stock i ; (subscript 1 refers to shrimp; subscript 2 refers to bottomfish, ij). When the stocks are in equilibrium (P_i^*), then

$$P_i^* = \frac{(a_i - q_i f)(b_j d_j k_j C_{jj} q_j f) + (a_j - q_j f)(d c_{ji} q_i f)}{(b_i - d_i c_{ii} q_i f)(b_j - d_j d_{jj} q_j f) - d_i d_j c_{ji} c_{ij} q_i q_j f^2} \quad (2)$$

The equilibrium biological production is (N_i^*)

$$N_i^* = P_i^*(a_i + d_j c_{ji} q_j f P_j^*) - (P_i^*)^2(b_i - d_i c_{ii} q_i f)$$

This model is characterized by the parabolic production function curve in which the maximum

equilibrium yield, when there is no discarding, occurs at population sizes which are one-half of their respective carrying capacities. In reality we expect that the production curve for shrimp would be exactly parabolic. Indeed density dependence implied by this model may not be readily demonstrated; the parabolic curve may be extremely flat in shrimp. Thus, parameter values were chosen to mimic this condition. However, we seek to determine the relative effect of the discard conversion terms on the shape of the production curves, *ie*, changes in maximum sustainable yield (MSY), changes in the effort required to produce MSY, and changes in the population size at MSY. Note that (1) assumed that there is no direct competition or predation between P_1 and P_2 . Interaction occurs only indirectly through the consumption of discards. As we discussed previously in this paper, evidence of competition and/or predation between shrimp and bottomfish is not clear cut. We will discuss the possible effects of these factors subsequently.

Parameterization

The production parameters assumed for equation (1) were chosen as follows: $a_1 = a_2 = b_1 =$

$q_1 = 1$; $b_2 = q_2 = 0.5$. This particular choice of parameters implies several relationships for the two stocks: when there is no discarding ($d_i = d_j = 0$); the biomass of bottomfish when there is no fishing is twenty times that of shrimp $P_{2\max} = 20.0$; $P_{1\max} = 1.0$); the maximum sustainable yield of bottomfish is twenty times that of the shrimp ($MSY_2 = 5.00$; $MSY = 0.25$); MSY for both are 25 percent of their respective carrying capacities. Also, bottomfish MSY occurs at population size of 10.0 and effort of 1.0 ($P_2^* = 10.0$, $f = 1.0$); whereas for shrimp it is $P_1^* = 0.5$, $f = 0.5$. The relative scale of these population parameters approximately corresponds to the ratio of shrimp and bottomfish catches observed.

Several alternatives were chosen for the discard and biological conversion rates d_i and c_{ij}). These alternatives span a range which we feel is ecologically meaningful. Note that these two rates act in tandem in the model to increase production. Thus, the effect on the population dynamics may be considered to be one parameter ($d_i c_{ij}$). The values of d_i which we used ranged from 0.0 to 1.0, *ie* discard rates of zero percent to 100 percent. The alternatives for c_{ij} which we tested in the model were $c_{ij} = 0.005$ or $c_{ij} = 0.01$. These imply that the assimilation of discard biomass *per unit biomass* of the stock is either 0.5 percent or 1.0 percent. For example, if the stock size of bottomfish is 15.0 and for shrimp it is 0.5 and all shrimp are discarded, then the ratio of additional biomass assimilated by bottomfish to the shrimp discards is approximately ten percent. This agrees with a trophic efficiency of ten to twenty percent that is often hypothesized in ecological literature (Ryther, 1969). However, the above assumes that there are no sources of forage

other than discards. This is, of course, untrue; therefore, we expect that these parameters are overestimated. We will discuss the ramifications of this bias later.

Results of the discard analysis

The parameter sets described were tested in the discard model and optimum effort (f_{opt}) calculations were generated numerically. In these results we report on six combinations of the parameters, which span the outcomes for the parameter ranges (Tables 6 and 7). Note that yield is the difference between biomass caught and biomass discarded. Therefore, the maximum equilibrium production ($MGP_i = \max N_i^*$), will be larger than the maximum equilibrium yield (MSY_i) by a factor of $1/(1 - d_i)$.

The net effect of discarding of catch and then its reassimilation into the population is an increase in the maximum productivity of the populations and the shift of the maximum to higher population and effort levels than in the no discard case. If there are no discards of shrimp and a large discard rate of bottomfish (*eg*, Table 7: Case II), then the reassimilation can be directly translated into shrimp yield. However, in the above case in which reassimilation rates are probably higher than expected, the increase in yield is only eight percent. Other discarding practices may increase shrimp productivity, but yield is reduced by the amount discarded to levels below the no discard situation (see Table 7: Cases III and VII). Additionally, the shrimp population size which produces the maximum productivity for a given discard policy only increases by a maximum of three percent (Case II). Similarly, the maximum effort increase (at shrimp MSY) is only

Table 6
DESCRIPTION OF ALTERNATIVE PARAMETER SETS TESTED IN DISCARD MODEL

Production Parameters (constant throughout this analysis)	
$a_1 = 1.0$; $b_1 = 1.0$; $a_2 = 1.0$; $b_2 = 0.05$; $q_1 = 1.0$; $q_2 = 0.5$	
Discard Parameters	
Case I:	No discards $d_1 = d_2 = 0$
Case II:	No discards of shrimp, high discard rate for bottomfish; high conversion by shrimp and bottomfish $d_1 = 0.0$; $d_2 = 1.0$; $c_{11} = c_{21} = c_{12} = c_{22} = 0.10$
Case III:	Low discard rate for shrimp; high discard rate for bottomfish; low conversion rates by shrimp; and by bottomfish $d_1 = 0.1$; $d_2 = 1.0$; $c_{11} = c_{21} = 0.005$; $c_{12} = 0.005$
Case IV:	High discard rate for shrimp; moderate discards for bottomfish low conversion by shrimp; and by bottomfish $d_1 = 0.5$; $d_2 = 0.5$; $c_{11} = c_{21} = 0.005$; $c_{12} = c_{22} = 0.01$
Case V:	High discard rate for shrimp; moderate discards of bottomfish; high conversion by shrimp; high conversion by bottomfish $d_1 = 0.5$; $d_2 = 0.5$; $c_{11} = c_{21} = 0.01$; $c_{12} = c_{22} = 0.01$
Case VI:	Low discard rate for shrimp; high discards of bottomfish; high conversion by shrimp; high conversion by bottomfish $d_1 = 0.1$; $d_2 = 1.0$; $c_{11} = c_{21} = 0.01$; $c_{12} = c_{22} = 0.01$
Case VII:	Low discard rate for shrimp; high discards of bottomfish; high conversion by shrimp; low conversion by bottomfish $d_1 = 0.1$; $d_2 = 1.0$; $c_{11} = c_{21} = 0.01$; $c_{12} = c_{22} = 0.005$

Table 7

IMPACT OF DISCARDING PRACTICES ON PRODUCTION OF MODEL SHRIMP AND BOTTOMFISH POPULATIONS (EQUATION (1)). SEE TEXT FOR DETAILS OF MODEL AND DEFINITION OF NOTATION. PARAMETER ALTERNATIVES ARE DESCRIBED IN Table 6. NOTE SUBSCRIPT 1 REFERS TO SHRIMP AND 2 REFERS TO BOTTOMFISH. ALSO MGP_1 IS THE MAXIMUM EQUILIBRIUM BIOLOGICAL PRODUCTION FOR STOCK i ($MGP_1 = \max N_1^*$)

Parameter Alternatives	Shrimp Maximization					Bottomfish Maximization						
	MSY_1 at MGP_1	P_1 given MGP_1	f given MGP_1	P_2 given MGP_1	N_2^* given MGP_1	Y_2 given MGP_1	MSY_2 at MGP_2	P_2 given MGP_2	f given MGP_2	P_1 given MGP_2	N_1^* given MGP_2	Y_1 given MGP_2
Case I: No discards	0.250	0.500	0.500	0.250	3.750	3.75	5.00	10.000	1.000	5.000	0	0
Case II: $d_1 = d_2 = 0$	0.270	0.515	0.525	0.270	4.128	0	0	10.615	1.050	5.573	0.006	0.006
Case III: $d_1 = 0; d_2 = 1.0$	0.233	0.500	0.520	0.260	3.951	0	0	10.28	1.025	5.267	0	0
Case IV: $d_1 = d_2 = 0.5$	0.128	0.500	0.510	0.255	3.852	1.926	2.565	10.157	1.010	5.129	0.003	0.001
Case V: $d_1 = d_2 = 0.5$	0.131	0.501	0.520	0.261	3.958	1.979	2.643	10.327	1.020	5.267	0.006	0.003
Case VI: $d_1 = 0.1; d_2 = 1.0$	0.244	0.503	0.540	0.271	4.169	0	0	10.615	1.050	5.573	0.006	0.005
Case VII: $d_1 = 0.1; d_2 = 1.0$	0.234	0.501	0.520	0.260	3.902	0	0	10.157	1.010	5.129	0.016	0.014

eight percent (Case VI). The effect of discard policy on bottomfish MSY's are similar. However, note that harvesting bottomfish at levels approximating MSY with a gear common to shrimping would likely cause overexploitation of the shrimp.

The qualitative results in Table 7 show the minimal effect of reassimilation of discards on shrimp and bottomfish productivity. The results are based, of course, on a rather arbitrary choice of the reassimilation rates and discard rates. Specifically, we have assumed that all of the discards were dead. If some were released alive, then effectively the reassimilation rate would be underestimated. However, it is unlikely that a significant number of discards are in fact released alive. We also assumed that the discards were converted (at a rate of 0.5 or 1.0 percent) only to shrimp or bottomfish biomass. We did not consider the consumption by populations other than shrimp and bottomfish. Our estimates represent an upper bound. If consumption by other species occurs, our estimates are too high, and the impact of reassimilation of discards is even less than presented in Table 7.

In general shrimp production is likely to be dominated by environmental influences, which cause large variations in year class strength. Thus it is unlikely that reassimilation of discards would be detectable using fisheries related data. Additionally, any benefits of altering management strategies to account for the reassimilation would also be undetected.

There are at least two aspects of shrimp and bottomfish interaction which were not considered in this analysis. The first is the effect of gear saturation. For example, culling large quantities of bottomfish from the shrimp catch may effectively reduce the catchability of the shrimp stocks. This could be incorporated into equation (1). The net effect of gear saturation caused by an increased biomass of another stock would reduce the maximum sustainable yield and the effort which produces it. Any regulation or gear development which might alter the stock size of bottomfish would thus affect the production of shrimp. At this point we make no suppositions as to the strength of this relationship.

Another important interaction is the effect of predation. Although we have noted in the previous section that predation rates of bottomfish on shrimp are probably small, the disparate magnitudes of their biomass may cause a significant effect. We will evaluate the possible effects of predation and other forms of interaction through an alternative model in the next section.

Energy-flow model of shrimp – bottomfish ecosystem

An energy-flow ecosystem model was developed to quantify the present role of bottomfish discards in the north-central Gulf of Mexico ecosystem and to evaluate the changes that might occur should discards be reduced. The fish discards of the shrimp fishery are generally viewed as a wasted resource (Technical Consultation on Shrimp By-catch Utilization, 1982). Regulations to reduce the quantity of discards have been implemented in some parts of the world (*ie* Guyana and Indonesia) and have been considered for the U S Gulf of Mexico (GMFMC, 1981). Because the volume of fish now captured in shrimp nets and thrown back to sea is so great in the north-central Gulf of Mexico, any reduction in the magnitude of what is captured or discarded may cause changes in other parts of the system and may even affect shrimp stocks and shrimp harvests.

Two methods of reducing discards have been considered by the Gulf of Mexico Fishery Management Council (GMFMC, 1981). The first is to utilize a greater portion of the by-catch. The second is to catch fewer fish by employing a specially-designed trawl with a lower catch-efficiency for bottomfish. The first would decrease the amount of dead fish returned to the system. The second would result in less dead fish and more living fish in the system. The ecosystem model was designed to test the theoretical effect of reducing discards by either of these methods.

The first step in the modeling effort was to draw a diagram depicting all the major components of the system and their relationships (*Figure 1*). The model system consists of 12 compartments, 11 of which represent trophic groups, in terms of biomass. The compartments are related by one-way flows of energy, primarily occurring as the feeding of one trophic group upon another, indicated by connecting lines. All possible trophic interactions between commercial penaeid shrimp, bottomfish, and other species of this system are covered. Fishery harvests of shrimp, bottomfish, menhaden (pelagic fish), and mackerels (migratory pelagics) are also included. The discard of bottomfish by shrimp vessels is indicated by the line leading from the bottomfish compartment to the compartment of high nitrogen organic material. High-nitrogen organic material, solely of animal origin, is distinguished from low-nitrogen organic material, consisting mainly of terrestrial plants that have been washed into the sea and phytoplankton that has sunk to the bottom. High-

nitrogen organic material, low-nitrogen organic material, and the benthic organisms that feed on them are the food sources of shrimp shown in the model. Bottomfish feed on these same foods, as well as on shrimp.

The compartments of the system are connected not only by trophic relationships but also by the cycling of nitrogen and other essential minerals. These nutrients, which stimulate primary production, are initially incorporated into living tissue by the phytoplankton and are then passed up the food chain, from which they are gradually remineralized and released, again becoming available to primary producers. The remineralization and release of nitrogen from animal groups and dead organic material is indicated in the diagram by dotted lines.

Several possible ways that shrimp standing stocks could be affected by reducing discards are obvious from the model diagram (*Figure 1*). If discards were reduced through either greater utilization of the by-catch or the use of trawls with a lower catch-efficiency for fish, the quantity of dead fish flesh available as food to shrimp would be lower. Additionally, the rate of remineralization and release from dead fish flesh of nitrogen and other nutrients essential to primary productivity would be lower. This might reduce the rate of production of phytoplankton, which, when it sinks to the bottom, becomes shrimp food.

The connecting lines representing trophic relationships indicate that bottomfish stocks could interfere with shrimp stocks through both predation and competition. Bottomfish not only prey on shrimp to at least some extent (although gut analyses suggest that the rate per fish is very low) but also feed on the same food eaten by shrimp. Changing the biomasses of either living or dead bottomfish in the system could have other indirect effects on shrimp that are not readily apparent from looking at the model diagram but may be observable from model simulations.

The model assumes that shrimp stocks and the other plant and animal stocks in the system are resource limited. Although there are no data directly relating shrimp production by natural systems to food supplies, the location of major fisheries in areas of the world's oceans where either primary productivity is high or the production of widespread areas is concentrated suggests that most, if not all, fisheries are resource limited.

The second step in model development was to quantify the compartments and flows of energy (as biomass) and nitrogen. The model was quantified for steady-state (inputs = outputs) conditions using an iterative top-down flow-balancing proce-

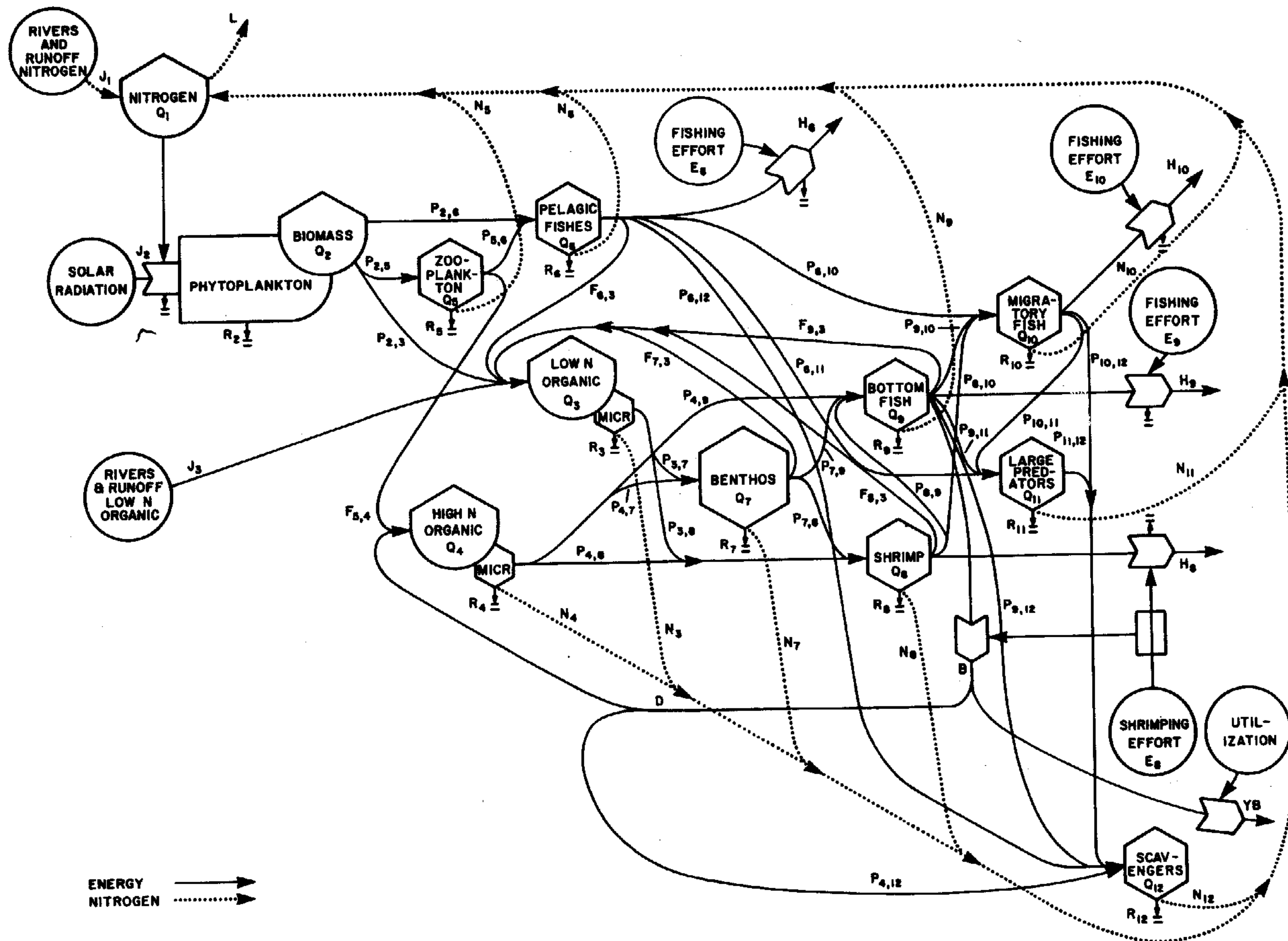


Fig 1 Energy-flow diagram of north-central Gulf of Mexico nearshore marine ecosystem

ture in which feeding flows to each animal compartment were calculated on the basis of total outflows from that compartment, including respiration, harvests, and predation (Browder, 1983).

The procedure started with the highest trophic level in the system and worked backward from the direction of energy flow. Feeding flows to a predator from alternative food sources were assumed to be proportional to the relative biomasses of these sources, except in cases of selectivity. Selectivity was approximated by the differential 'weighting' of two or more feeding flows to the same predator.

Essential inputs for calculating feeding flows

and setting rate coefficients by this method were (1) biomass of each trophic group, (2) respiration rate coefficients of each animal group, (3) either the respiration rate coefficient or outside flows to each food-chain-base compartment (*ie* phytoplankton and low-nitrogen organic material), (4) assimilation coefficient for each type of food of each predator, and (5) selectivity weighting factors for alternative prey of each predator. Values entered into the model (not calculated by the flow-balancing procedure) are given with derivation in *Tables 8 and 9*.

Assigned weighting factors (*Table 9*) were on a scale of 0.001 to 1.0, with 0.001, when used with

Table 8
INITIAL DRY WEIGHTS (Q) (MG/M^2), EXOGENOUS INFLOW (J) ($\text{MG}/\text{M}^2 \cdot \text{DAY}$), RESPIRATION RATE COEFFICIENTS (C_R) ($\text{MG}/\text{MG WEIGHT} \cdot \text{DAY}$), AND HARVESTING RATE COEFFICIENTS (C_H), ($\text{MG}/\text{MG WEIGHT} \cdot \text{DAY}$), BODY NITROGEN/DRY WEIGHT RATIOS (C_N), AND RATIOS OF NITROGEN RELEASED IN EXCREMENT TO ORGANIC MATTER BURNED IN METABOLISM (B)

		Q	J	C_R^a	C_H^b	C_N^c	B
1	Nitrogen	1 260.0 ^d	112 ^p				
2	Phytoplankton	1 125.0 ^e	2 711 ^q	0.768 ^s			0.06 ⁱⁱ
3	Low-nitrogen organic material	218 850.0 ^f	3 037 ^r	0.01872 ^t		0.05 ^{gg}	
4	High-nitrogen organic material	33.4 ^g		0.2071 ^u		0.0756 ^{hh}	
5	Zooplankton	145.9 ^h		0.32 ^v		0.0165 ^c	0.073 ^{ji}
6	Pelagic fish (menhaden)	2 966.0 ⁱ		0.020 ^w	0.01389 ^{dd}	0.0453 ^c	0.0924 ^{kk}
7	Benthos	8 000.0 ^j		0.081 ^x		0.0353 ^c	0.1202 ^{ll}
8	Shrimp	79.4 ^k		0.0414 ^y	0.002778 ^{dd}	0.0959 ^c	0.1083 ^{mm}
9	Bottomfish	2 011.0 ^l		0.018 ^z	0.0004061 ^{ee}	0.1159 ^c	0.1297 ⁿⁿ
10	Migratory pelagics (mackerel)	32.4 ^m		0.006 ^{aa}	1.023 $\times C_{H8}^{ff}$	0.1023 ^c	0.1250 ^{oo}
11	Large predators (dolphin)	6.6 ⁿ		1.38 ^{bb}		0.1096 ^c	0.1308 ^{pp}
12	Large scavengers (sharks)	24.3 ^o		0.0068 ^{cc}		0.1098 ^c	0.1445 ^{qq}

^a $Q \times C_R = R$ = respiration rate

^b $Z \times C_H = H$ = harvesting rate

^c $R \times C_N = N$ = nitrogen release rate. The nitrogen release rate was assumed to be proportional to respiration of animals (and of the microbes decomposing organic material). C_N values were estimated from body nitrogen/dry organic matter ratios by calculating steady state nitrogen flows corresponding to steady state organic matter flows. In the calculations, nitrogen not used in growth or predation was divided between excrement and feces in the proportions 0.8 and 0.2, respectively, in all animals except zooplankton. For zooplankton, the apportionment was 0.2 for excrement and 0.8 for feces to reflect the high-nitrogen concentration of zooplankton fecal pellets suggested by the literature. C_{N3} (the coefficient for low-nitrogen organic material) was estimated rather than calculated in the above manner.

^d from concentration of inorganic nitrogen ($\text{NO}_2\text{—N}$ and $\text{NO}_3\text{—N}$) in waters offshore of the Mississippi Delta (126 mg/m^3) (Sklar, 1976) and estimated depth of photic zone (10 m)

^e from concentration of chlorophyll *a* offshore Mississippi Delta (18 mg/m^2) (Sklar, 1976), ratio of carbon to chlorophyll (25) (Parsons *et al.*, 1977), and ratio of dry organic matter to carbon (2.5) (Parsons *et al.*, 1977).

^f from concentration of dry organic material in shallow-water Mississippi Delta marine sediments (10 mg/g) (Hausknecht, 1980); depth of sediment in which more than 80% of megafauna occurs (3 cm) (Tietjen, 1969); and weight of inorganic fraction per centimeter thick square meter area, calculated by method of Bennett and Lambert (1977), assuming specific gravity of 2.7 for Mississippi Delta sediments (Bennett, pers. comm., for clay).

^g estimated to be equal to daily flow of zooplankton fecal pellets and discards.

^h from number of individuals per unit volume (2 432/ m^3) (Reitsema, 1980), dry weight per individual (6×10^{-3} mg) (Conover, 1959) and estimated depth of photic zone.

ⁱ Louisiana menhaden landings in 1975 (4.5×10^{14} mg), assumed ratio of all coastal herring to menhaden (2), dry weight/wet weight ratio (0.2) (Parsons *et al.*, 1977) and assumed annual fishing mortality of 1.0; divided by Louisiana bottom area inside 93 meters (50 fathoms).

^j from Parker *et al.* (1980).

Table 8 (continued)

INITIAL DRY WEIGHTS (Q) (MG/M^2), EXOGENOUS INFLOW (J) ($\text{MG}/\text{M}^2 \cdot \text{DAY}$), RESPIRATION RATE COEFFICIENTS (C_R) ($\text{MG}/\text{MG WEIGHT} \cdot \text{DAY}$), AND HARVESTING RATE COEFFICIENTS (C_H), ($\text{MG}/\text{MG WEIGHT} \cdot \text{DAY}$), BODY NITROGEN/DRY WEIGHT RATIOS (C_N), AND RATIOS OF NITROGEN RELEASED IN EXCREMENT TO ORGANIC MATTER BURNED IN METABOLISM (B)

- ^k Louisiana shrimp landings in 1975 (2.41×10^{13} mg), converted to dry weight (0.2) and divided by Louisiana bottom area inside 93 meters ($6.069 \times 10^{10} \text{m}^2$) (Patella, 1975).
- ^l estimated bottomfish catch, including discards, in 1975, for area inside 93 meters from Pt. Au Fer, Louisiana, to Perdido Bay, Florida (430×10^{12} mg); converted to dry weight (0.2); multiplied by an assumed annual fishing mortality of 0.8; and divided by area ($3.42 \times 10^{10} \text{m}^2$) (Patella, 1975).
- ^m from annual U S king and Spanish mackerel landings in 1975 (2.27×10^{12} mg and 4.5×10^{12} mg) (NMFS, 1978); king and Spanish mackerel annual fishing mortality (0.41 and 0.2756) (GMSAFMC, 1980); estimated fraction of total mackerel stocks that occur in the Gulf of Mexico (0.67) ratio of total migratory biomass to mackerel biomass (2.0), dry weight-wet weight conversion (0.2) and estimated bottom area of Gulf of Mexico inside 93 meters (50 fathom) ($1.81 \times 10^{11} \text{m}^2$) (Patella, 1975).
- ⁿ from density of bottlenose dolphin at Louisiana coastal sites (0.44×10^{-6}) (Leatherwood *et al.*, 1978), estimated average weight of bottlenose dolphin (150 kg wet weight), dry weight to wet weight conversion (0.2), and factor to correct for better-than-average densities thought to have occurred in sampling area (0.5).
- ^o estimated average biomass of elasmobranchs in Gulf of Mexico ($24.29 \text{ mg}/\text{m}^2$) (L. Rivas, Nova University, Ft. Lauderdale, FL, pers. comm.), converted to dry weight (0.2), and multiplied by an assumed near-shore concentration factor of 5.
- ^p concentration of inorganic nitrogen in Mississippi River water ($2000 \text{ mg N}/\text{m}^3$) (Sackett, 1972) times rate of freshwater inflow from Mississippi and Atchafalaya Rivers ($1.9 \times 10^9 \text{ m}^3/\text{day}$) (Sackett, 1972), divided by estimated area of bottom under the immediate influence of Mississippi and Atchafalaya discharge ($3.42 \times 10^{10} \text{m}^2$).
- ^q rate of gross primary productivity, equal to net primary productivity per unit weight (1.642) (Sklar, 1976) plus respiration rate coefficient (0.768) (Ryther and Guillard, 1962), multiplied by phytoplankton biomass.
- ^r estimated annual carbon export from Barataria Bay per square meter of inshore water ($15 \times 10^4 \text{ mg C}$) (Happ *et al.*, 1977) times Louisiana inshore water area ($1.367 \times 10^{10} \text{m}^2$) (Perret *et al.*, 1971), divided by Louisiana offshore water area to 93 m; plus concentration of dissolved organic carbon in Mississippi River water (20 mg/liter) times annual volume of Mississippi and Atchafalaya discharge (6.9×10^{14} liters/day), divided by area inside 93 m from Pt. Au Fer, LA, to Perdido Bay, FL ($3.42 \times 10^{10} \text{m}^2$)—all multiplied by 2.5 to convert carbon to organic matter and divided by 360 to express in terms of days.
- ^s Ryther and Guillard (1962) for 4, eurythermal diatom (*Cyclotella nana*, 3H).
- ^t set in flow-balancing procedure to approximate value for zooplankton fecal pellet decomposition calculated from Johannes and Satomi (1966) (0.1834).
- ^u calculated in flow-balancing procedure.
- ^v Conover (1959) for 6 g D. W. copepod.
- ^w Hettler (1976) for 226 g W. W. menhaden.
- ^x Pamatmat (1980) 1 g W. W. (assumed $20 \times$ anaerobic rate).
- ^y Bishop *et al.* (1980) for 6.7 g brown shrimp (assumed 12 hrs activity).
- ^z Hoss (1974) for 100 g pinfish.
- ^{aa} Brill (1979) for 1 kg skipjack tuna.
- ^{bb} Irving *et al.* (1941) for 150 kg bottlenose dolphin.
- ^{cc} Brett and Blackburn (1978) for 900 g spiny dogfish.
- ^{dd} based on landings (NMFS, 1978).
- ^{ee} harvesting coefficient for directed fishery, based on landings (NMFS, 1980).
- ^{ff} harvesting coefficient for bycatch, based on estimated discards (GMFMC, 1980) (by-catch is proportional to the harvesting rate coefficient for shrimp).
- ^{gg} estimate for river detritus.
- ^{hh} calculated for initial mix of zooplankton fecal pellets and fish flesh.
- ⁱⁱ Strickland (1960) for mixed taxa.
- ^{jj} Parsons *et al.* (1977) for zooplankton.
- ^{kk} Sidwell (1981) for menhaden.
- ^{ll} Darnell and Wissing (1975).
- ^{mm} Sidwell (1981) for commercial penaeid shrimp.
- ⁿⁿ Darnell and Wissing (1975) for pinfish.
- ^{oo} estimated from a value for mackerel from Sidwell (1981) for muscle tissue only.
- ^{pp} Sidwell (1981) for bottlenose dolphin muscle.
- ^{qq} Sidwell (1981) for *Sphyrna blochii* muscle.

NOTE: Constants used in the model but not shown on the table are given below with information sources.

- K_{m1} (Michaelis-Menten coefficient for the effect of inorganic nitrogen concentration on phytoplankton production) = 120 (based on a half-saltwater constant of 1.5 moles-liter for *Asterionella japonica*, a coastal diatom, as determined by laboratory experiments of Eppley and Thomas (1969). K_{m1} occurs in the equation for calculating J_2).
- K (coefficient for loss of nitrogen from the system in currents and by denitrification) = 0.189 (calculated for steady state conditions (inflows = outflows) on basis of inflows and other outflows. L , rate of loss of nitrogen from the system, is equal to $Q_1 \times K$. For initial conditions, $L = 238$).

Table 9
ASSIMILATION COEFFICIENTS (A) AND WEIGHTING FACTORS (W) FOR NORTH CENTRAL GULF OF MEXICO ECOSYSTEM MODEL (VALUES NOT FOOTNOTED WERE ASSUMED)

FROM	1		2		3		4		5		6		7		8		9		10		11		12	
TO	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W	A	W
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	0.70 ^a	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	0.42	1.0	-	-	-	-	0.6	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	0.5	0.008 ^e	0.9	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	0.2 ^b	0.001	0.4 ^c	1.0	-	-	-	-	0.4 ^c	1.0	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	0.86 ^d	1.0	-	-	-	-	0.7	1.0	0.86 ^d	1.0	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	0.8	1.0	-	-	-	-	0.7	1.0	1.0	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	0.8	1.0	-	-	-	-	-	-	1.0	1.0	0.7	1.0	-	-	-	-
12	-	-	-	-	-	-	-	-	0.8	0.1	-	-	-	-	-	-	1.0	0.1	1.0	0.1	1.0	0.001	-	-

^a Parsons *et al* (1977) for copepods.

^b Jones (1973) for brown shrimp, away from shore.

^c Jones (1973) for brown shrimp, at edge of shore.

^d Darnell and Wissing (1975) for polychaetes consumed by pinfish.

^e Approximated in calculation to set the respiration rate coefficient for high-nitrogen organic material.

1.0 for alternative prey, indicating intense selection against a prey type. Absence of selectivity was indicated by assigning a weighting factor of 1.0 to all prey of the same predator. Assignment of weighting factors was based on qualitative information about a predator and its alternative prey. In the initial quantification of the model, weighting factors were set so that all organisms feeding on low-nitrogen organic material selected against this food in favor of alternatives and so that large scavengers selected dead fish over living prey. Otherwise, all weighting factors were set at 1.0. Although the low frequency of shrimp in the stomach contents of bottomfish—even those caught in trawls with shrimp—suggests that bottomfish may concentrate on other organisms, the model was initially quantified to indicate no selectivity against shrimp in order that the worst possible condition of predation by bottomfish on shrimp might be evaluated.

Initial values for all flows of energy and nitrogen in the system, most of which were calculated by the flow-balancing procedure, are given in *Table 10*. Flows to and from the inorganic nitrogen (Q_1) high-nitrogen organic material (Q_4), benthos (Q_7), shrimp (Q_8), and bottomfish (Q_9) compartments are directly relevant to evaluating the effect of reducing bottomfish discards on shrimp biomass and harvests. (Other flows may have indirect effects, but these can only be evaluated with simulations.)

The nitrogen compartment received inflows from river and runoff (J_1), from the microbial

breakdown of low-nitrogen organic material (N_3), from the breakdown of high-nitrogen organic material (N_4), and in animal excrement (N_5 to N_{12}). Outflows were uptake by phytoplankton, in association with their growth ($P_{1,2}$), and losses to the system in currents (L). The major contribution was from the remineralization of low-nitrogen organic material, most of which entered the system in rivers and as coastal runoff. This contribution was more than two orders of magnitude higher than that from the breakdown of high-nitrogen organic material, approximately half of which was made up of discards. The combined contribution from animal excrement was also more than two orders of magnitude greater than that from high-nitrogen organic material. Recycling from animals alone was almost sufficient to satisfy the daily phytoplankton uptake rate, although it might not have been adequate to promote maximum photosynthesis. Nitrogen in river and runoff waters also was sufficient to replenish nitrogen taken up in daily growth of phytoplankton at the calculated rate. The quantity of nitrogen released from discards and other high-nitrogen sources was less than one one-thousandth the stock of inorganic nitrogen in the environment.

In the model, shrimp received energy from three sources: benthos (Q_7), low-nitrogen organic material (Q_3), and high-nitrogen organic material (Q_4). Despite the fact that high-nitrogen organic material was weighted 1 000 to 1 over low-nitrogen organic material, the latter was 50 times more important as a food source of shrimp [25 times

Table 10

MATRIX OF INITIAL STEADY-STATE FLOW FROM SOURCES TO COMPARTMENTS, FROM COMPARTMENTS TO SINKS, AND BETWEEN COMPARTMENTS.^{a,b}
(FLOW RATES WERE CALCULATED IN THE ITERATIVE TOP-DOWN FLOW-BALANCING PROCEDURE, UNLESS OTHERWISE INDICATED)

To	From Source	Q1	Q2	Q3	Q4	Q5	Q6	Q7	Q8	Q9	Q10	Q11	Q12	Organic	Nitrogen
Sinks ^{c,d}	—	(238.6) ^e	864	4 102	6.984	46.69	59.32	648.0	3.288	36.00	0.1944	9.108	0.1657	5 776	(238.6)
Harvest ^d	—	—	—	—	—	—	4.119	—	0.2206	0.8112	0.0209	—	—	—	(349.4)
Q1	(112.0)	—	—	(205.1)	(0.5280)	(0.7694)	(2.687)	(22.83)	(0.3198)	(4.169)	(0.0199)	(0.9980)	(0.0182)	—	(110.8)
Q2	2 711	(110.8) ^{d,e}	—	—	—	—	—	—	—	—	—	—	—	—	—
Q3	3 037	—	1 614	—	—	27.81	88.69	690.7	6.208	7.724	0.0395	1.226	0.0220	5 473	—
Q4	—	—	—	—	—	—	—	—	—	5.686 ^{d,g}	—	—	—	5.686	—
Q5	—	—	92.70	—	—	—	—	—	—	—	—	—	—	92.70	—
Q6	—	—	140.4	—	—	18.20	—	—	—	—	—	—	—	158.6	—
Q7	—	—	—	1 376	26.25	—	—	—	—	—	—	—	—	1402.3	—
Q8	—	—	—	0.2720	0.0415	—	—	9.942	—	—	—	—	—	10.26	—
Q9	—	—	—	—	0.2246	—	—	53.80	0.5341	—	—	—	—	54.56	—
Q10	—	—	—	—	—	—	0.1899	—	0.0051	0.1280	—	—	—	0.3230	—
Q11	—	—	—	—	—	—	6.132	—	—	4.135	0.0670	—	—	10.33	—
Q12	—	—	—	—	0.0021	—	0.1101	—	—	0.0743	0.0012	0.0000025	—	0.1877	—
Total organic matter	5 748	—	2 711	5 478	33.50	92.70	158.5	1 402	10.26	564.56	0.3230	10.33	0.1877	25 700	—
Total nitrogen	(112.0)	(349.4)	—	(205.1)	(0.5280)	(0.7694)	(2.687)	(22.83)	(0.3198)	(4.169)	(0.0199)	(0.9980)	(0.0182)	—	(699)

^a Q1 = nitrogen

Q2 = phytoplankton

Q3 = low-nitrogen organic material

Q4 = high-nitrogen organic material

Q5 = zooplankton

Q6 = pelagic forage fish (menhaden)

Q7 = benthos

Q8 = commercial penaeid shrimp

Q9 = bottomfish

Q10 = coastal pelagics (mackerels)

Q11 = marine mammals (dolphin)

Q12 = large scavengers (sharks)

^b Values are milligram dry weight per square meter per day, except those in parentheses, which are milligrams nitrogen per square meter per day.^c Respiration rates in milligrams dry organic matter equivalent per day.^d Values independent of flow-balancing procedure unless otherwise indicated.^e Loss of nitrogen from system in currents and denitrification, calculated by flow balancing.^f Uptake of nitrogen by phytoplankton in photosynthesis.^g Discards.

more important if the different assimilation rates (Table 10) are considered]. Benthos, which was weighted equally with high-nitrogen organic material as a food source, was 200 times more important, according to flow rates. Bottomfish fed on the same types of food eaten by shrimp. The flow of each to bottomfish was approximately five times greater than the flow to shrimp.

Energy flowed from the shrimp compartment (Q_8) in predation by bottomfish (Q_9), predation by migratory pelagics (Q_{10}), harvests of man, and respiration. Predation by bottomfish was three times the harvest rate and one-fifth the respiration rate of shrimp. The flow of energy from shrimp to bottomfish was two orders of magnitude lower than the flow of energy to bottomfish from the benthos (Q_7).

The rate of predation of bottomfish on shrimp in the model was highly dependent upon the weighting factors for bottomfish feeding on alternative prey. Variation in the calculated predation rate was directly proportional to the ratio of the weighting factor for shrimp to that of the alternative prey. Predation rates of bottomfish on shrimp were 0.0538, 0.00538, and 0.000538 for shrimp weighting factors of 0.1, 0.01, and 0.001 respectively (weighting factors for alternative prey were 1.0).

The third step in model development was write a computer program in which the mathematical relationships suggested by the model diagram were incorporated into a set of integral (Euler numerical integration) equations. In these equations, all flow rates to animal compartments were donor-recipient controlled and of the form:

$$P = c_{ij}Q_iQ_j,$$

where c was the rate coefficient, Q was compartment, i indicated prey, and j indicated predator. Gross primary productivity was a function of the form:

$$J = S(Q/K_m + Q),$$

where S was maximum gross primary productivity, K_m was the nitrate-nitrogen content of the water at half maximum velocity, and Q was nitrogen. Nitrogen released in excrement or decomposition was a function of respiration rate and the nitrogen concentration in the source material. All other flows in the model were proportional to donor biomass or were simple algebraic relationships. A more detailed mathematical description of the model was given in Browder (1983).

The computerized model was used to simulate the biomasses of the trophic groups as they changed over time in response to a reduction in the

rate of discarding. The effect of reducing discards by each of the two suggested methods was tested by resetting one coefficient to approximate the test condition, after initially quantifying the flow rates for present steady-state conditions. For each test, the model was run for a simulated 5-yr period, iterating 10 times per day. Under test conditions, the biomasses, simulated over time, moved from initial steady-state levels to a new steady state, whereas, when the model was run for present conditions (not resetting either coefficient), biomasses were constant throughout the 5-yr period. The direction and magnitude of the change in steady-state biomasses indicated the effect of the test condition. In quantifying the model, inputs such as inorganic nitrogen and detritus were held constant over time to enable all changes in biomass levels to be attributable to the conditions being tested.

Using the computerized model, simulations of shrimp biomass were produced for two test conditions: (1) one-half of the by-catch utilized and (2) fish catch-efficiency of shrimp trawls reduced by one-half. The latter test was run twice, once with no selectivity against shrimp (shrimp weighting factor = 1.0) and, the second time, with moderate selectivity (shrimp weighting factor = 0.01) by bottomfish against shrimp.

Under the assumption of no selection against shrimp by bottomfish, a decrease in shrimp biomass resulted from decreasing bottomfish discards by either method. A 25 percent decrease occurred with by-catch utilization, whereas, when the special trawls were used, the decrease was only 8 percent. When moderate selectivity was assumed, results of reducing discards by the two methods diverged even more. The use of trawls with a lower catch efficiency for fish did not have a detrimental effect on shrimp biomass over the long term. In this simulation, shrimp biomass declined briefly but rebounded to former levels before the end of the second year. Although the higher biomass of bottomfish caused by decreased fishing mortality increased the pressure on shrimp from both predation and competition, this negative effect was outweighed by concurrent responses to the change elsewhere in the system that were beneficial to shrimp. The main factor appears to have been a chain of events beginning with an increase in marine mammal biomass resulting from the increased supply of bottom-fish prey. Marine mammals, having increased, fed more heavily on menhaden and other pelagic fish as well as on bottomfish, leading to a decline in pelagic fish biomass. The resultant reduction in predation

pressure on zooplankton by pelagic fish caused zooplankton to proliferate and produce more fecal pellets, increasing the supply of high-nitrogen food for shrimp.

The decrease in shrimp biomass that followed reducing discards by means of utilization of one-half the by-catch was due to a decrease in the supply of food for shrimp. (There had been no increase in either predation or competition, because fishing pressure on bottomfish had not been reduced.) The rate that shrimp fed on high-nitrogen organic material decreased by about one-third when utilization of one-half the by-catch was instituted. The rate that shrimp fed on low-nitrogen organic material also was slightly lower. Nitrogen remineralization decreased slightly when discarding was reduced through by-catch utilization and slightly depressed primary productivity in the model system, despite the large quantity of nitrogen entering the system in river water.

The nitrogen remineralization rate was greatest when shrimp trawls with reduced catch-efficiency for fish were used, suggesting that bottomfish promote a greater rate of remineralization when alive than dead. The increased remineralization associated with the use of gear with a lower efficiency for catching fish did not increase primary productivity—possibly because the system was already operating in close proximity to the nitrogen-saturation point. (Sensitivity tests of the effect of nitrogen-related variables on these results have not yet been performed.)

The compartments of this system are linked by many routes, and it was impossible to evaluate which pathways were causally important by merely looking at the diagram and by comparing the magnitudes of direct flow rates. Direct effects were, in some cases, outweighed by indirect effects that were not obvious from the diagram. The computer model kept track of flows throughout the system and allowed their net effects to be observed.

Model results, at this point, are highly theoretical. How well the model reflects the behavior of the real system remains to be determined. A weakness of the model is that it contains several parameters that have not been measured and could only be grossly estimated, or, in some cases, arbitrarily set. Further sensitivity testing is needed to determine the dependence of model results on these parameters, and field or laboratory studies are needed to quantify those parameters to which model results are sensitive. The demonstrated sensitivity of results to selectivity weighting factors points to the need to measure the rate of predation by bottomfish on shrimp and on alternative prey

relative to the biomasses of shrimp and the alternative prey in the habitats where they occur together.

Conclusions

The nature of shrimp and bottomfish interactions was evaluated using three approaches: 1) a biological review to define possible ecological connections; 2) a classical population dynamics approach to determine effects of discards on shrimp harvests, assuming that discards are a source of food to shrimp; and 3) an energy-flow model to evaluate the effect on shrimp stocks of changing discard practices, given the multiple connections between shrimp, bottomfish, and the other components of the ecosystem.

The biological review revealed that only a few quantitative studies of the stomach contents of bottomfish species have been performed and most did not separate commercial penaeid shrimp from other penaeids. The limited information available indicated a low-frequency of occurrence of commercial penaeid shrimp in the stomachs of bottomfish species and suggested that man may be the major predator of these penaeids.

The population dynamics model suggested that even the discard practices most favorable to shrimp would increase shrimp harvests only 8% over the case with no discards. Since assimilation rates in the model were deliberately overestimated, the actual benefit of discards to shrimp production probably is less. Environmental 'noise' undoubtedly would prevent changes this small from being detected in fisheries data.

The hypothetical effect of interference with shrimping operations by an increased bottomfish stock was examined using a simple extension to the population dynamics model. The interference resulted in both a reduction in shrimp MSY and a reduction in the effort required to achieve MSY. No attempt was made to quantify these reductions, as this would require more extensive modeling of fishing operations.

The computerized energy-flow ecosystem model suggested that, theoretically, shrimp biomass would decline 25 percent if discards were reduced by utilization of one half the by-catch, but would decline by only 8 percent if discards were reduced through the use of new trawls one-half as efficient in catching fish. The 8 percent reduction occurred only if the 'worst case' of bottomfish predation on shrimp—no selectivity by bottomfish against shrimp—were assumed. The model predicted that, if moderate selection against shrimp by bottomfish were occurring, the introduction of special trawls

would result in no long term effect on shrimp stocks and shrimp harvests.

Initial model results indicated that determining the rate of predation by bottomfish on shrimp and on alternative prey relative to the biomasses of each in the environment may facilitate an understanding of shrimp and bottomfish interactions and the potential impact on shrimp of reducing bottomfish discards.

References

- ALLSOPP, W H L M S. Fish by-catch from shrimp trawling. The 1980 main protein resource for Caribbean Atlantic countries: reality and potential. Unpubl. report to the Inter-American Development Bank. Round Table on Non-traditional Fishery products for Mass Human Consumption, Washington, D.C., 15-19 Sept. 1980. 32 p.
- ARMITAGE, T M and ALEVIZON, W S. The diet of the Florida 1980 pompano (*Trachinotus carolinus*) along the east coast of central Florida. *Florida Sci.* 43:19-26.
- BASS, A J, D'AUBREY, and KISTNASAMY, N. Sharks of the east 1973 coast of southern Africa. I. The genus *Carcharhinus* (Carcharhinidae). So. Afr. Assoc. Mar. Biol. Res., Oceanogr. Res. Inst. Investig. Rep. No. 33. 168 p.
- BEARDEN, C M. A contribution to the biology of king whittings, 1963 genus *Menticirrhus*, of South Carolina. Contrib. Bears Bluff Lab. No. 38, 27 p.
- BEAUMARIAGE, D C. Age, growth, and reproduction of king 1973 mackerel, *Scomberomorus cavalla*, in Florida. Fla. Mar. Res. Publ. 1. Dept. Nat. Resources, Tallahassee. 45 p.
- BELL, J D, BURCHMORE, J J and POLLARD, D A. Feeding ecology 1978 of a scorpaenid fish, the fortescue *Centropogon australis*, from a *Posidonia* habitat in New South Wales. *Aust. J. Mar. Freshwat. Res.* 29: 175-186.
- BENNETT, R H and LAMBERT, D N. Rapid and reliable technique 1971 for determining unit weight and porosity of deep-sea sediments. *Mar. Geol.* 11: 201-207.
- BISHOP, J M, GOSSELINK, J C and STONE, J H. Oxygen consump- 1980 tion and hemolymph osmolality of brown shrimp, *Penaeus aztecus*. *Fish Bull.* 78: 741-757.
- BRADLEY, E and BRYAN, C E. Life history and fishery of the red 1975 snapper (*Lutjanus campechanus*) in the northwestern Gulf of Mexico: 1970-1974. *Proc. Gulf Caribb. Fish. Inst.* 27: 77-106.
- BRETT, J R and BLACKBURN, J M. Metabolic rate and energy 1978 expenditure in the spiny dogfish *Squalus acanthias*. *J. Fish Res. Bd. Canada* 35: 816-821.
- BRILL, R W. The effect of body size on the standard metabolic 1979 rate of skipjack tuna, *Katsuwonus pelamis*. *Fish. Bull.* 77: 494-498.
- BROWDER, J A. A simulation model of a near-shore marine 1983 ecosystem of the north-central Gulf of Mexico. In: Turgeon, K (Ed). *Marine Ecosystem Modeling. Procedures of a Workshop held April 6-8, 1982, Frederick, Maryland, NOAA (National Environmental and Satellite Data and Information Service) Publication.* Washington, D.C.
- BRUSHER, H A, RENFLO, W C and NEAL, R A. Notes on the 1972 distribution, size, and ovarian development of some penaeid shrimps in the northwestern Gulf of Mexico, 1961-1962. *Contrib. Mar. Sci.* 16: 75-87.
- CARR, W E S and ADAMS, C A. Food habits of juvenile marine 1973 fishes occupying seagrass beds in the estuarine zone near Crystal River Florida. *Trans. Amer. Fish. Soc.* 103: 511-540.
- CHAO, L N and MUSICK, J A. Life history, feeding habits, and 1977 functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. *Fish. Bull.* 75: 657-702.
- CONOVER, R J. Regional and seasonal variation in the respira- 1959 tory rate of marine copepods. *Limnol. Oceanogr.* 4: 259-269.
- DARNELL, R M. Food habits of fishes and larger invertebrates of 1958 Lake Ponchartrain, Louisiana, and estuarine community. *Pub. Inst. Mar. Sci. Univ. Texas* 5: 353-416.
- DARNELL, D M and WISSING, T W. Nitrogen turnover and food 1978 relationships of the pinfish *Lagodon rhomboides* in a North Carolina estuary. P 81-110. In: F. J. Vernberg (ed.). *Physiological ecology of Estuarine Organisms.* University of South Carolina Press, Columbia. 396 p.
- DIVITA, R, CREEL, M and SHERIDAN, P F. Foods of coastal fishes 1983 during brown shrimp *Penaeus aztecus*, migration from Texas estuaries. *Fish. Bull.* 81 (in press).
- DOOLEY, J K. Systematics and biology of the tilefishes (Per- 1978 ciformes: Branchiostegidae and Malacanthidae), with descriptions of two species. *NOAA Tech. Rept. NMFS CIRC-411.* 78 p.
- DRAGOVICH, A. Review of studies of tuna food in the Atlantic 1969 Ocean. *US Fish Wildl. Serv. Spec. Sci. Rept. Fish.* 593. 21 p.
- DRAGOVICH, W. The food of bluefin tuna (*Tunnus thynnus*) in 1970a the western North Atlantic Ocean. *Trans. Amer. Fish. Soc.* 99: 726-731.
- DRAGOVICH, A. The food of skipjack and yellowfin tunas in the 1970b Atlantic Ocean. *US Fish and Wildl. Service Fishery Bull.* 68: 445-460.
- DRAGOVICH, A and POTTHOFF, T. Comparative study of food of 1972 skipjack and yellowfin tunas off the coast of West Africa. *Fish. Bull.* 70: 1087-1110.
- EPPLEY, R W and THOMAS, W H. Comparison of half-saturation 1969 constants for growth and nitrate uptake of marine phytoplankton. *J. Phycol.* 5: 375-379.
- FONTENOT, F J, JR and ROGILLIO, H E. A study of estuarine 1970 sport fishes in the Biloxi marsh complex, Louisiana. *La. Wildl. Fish. Comm., F-8 Compl. Rep.* 172 p.
- FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED 1979 NATIONS. Catches and landings, 1978. *FAO Yearbook of Fishery Statistics, Vol. 46.* FAO, Rome, 372 p.
- FOX, L S and WHITE, C J. Feeding habits of the southern 1969 flounder, *Paralichthys lethostigma*, in Barataria Bay, Louisiana. *Proc. La. Acad. Sci.* 31: 31-38.
- GRIFFIN, W L and WARREN, J P. Costs and return data; 1978 groundfish trawlers of northern Gulf of Mexico. Unpubl. Report to Gulf of Mexico Fishery Management Council. Tampa, Florida.
- GRIMES, C B. Diet and feeding ecology of the vermilion 1979 snapper, *Rhomboplites aurorubens* (Cuvier), from North Carolina and South Carolina waters. *Bull. Mar. Sci.* 29: 53-61.
- GMFMC (Gulf of Mexico Fishery Management Council). 1980 Draft fishery management plan for groundfish in the Gulf of Mexico. Tampa, Fla.
- GMSAFMC (Gulf of Mexico and South Atlantic Fishery 1980 Management Council). Fishery Management Plan, Final Environmental Impact Statement, and Regulatory Analysis for the Coastal Migratory Pelagic Resources.
- GUNTER, G. Studies on marine fishes of Texas. *Publ. Inst. Mar. Sci. Univ. Texas* 1: 9-190.
- HAPP, G, GOSSELINK, J G and DAY, J W, JR. The seasonal 1977 distribution of organic carbon in a Louisiana estuary. *Estuarine Coastal Mar. Sci.* 5: 695-705.
- HARRIS, A H and ROSE, C D. Shrimp predation by the sea 1968 catfish, *Galeichthys felis*. *Trans. Amer. Fish. Soc.* 97: 503-504.
- HAUSKNECHT, K A. Describe surficial sediments and suspended 1980 particulate matter. Vol. V In: W. B. Jackson and G. M. Faw (eds.), *Biological/chemical survey of Texoma and Capline sector salt dome brine disposal sites off Louisiana, 1978-1979.* NOAA Tech. Mem. NMFS-SEFC-20, 56 p.
- HENWOOD, T, JOHNSON, P and HEARD, R. Feeding habits and 1978 food of the long-spined porgy, *Stenotomus caprinus* Bean. *Northeast Gulf Sci.* 2: 133-137.

- HETTLER, W F. Influence of temperature and salinity on routine metabolic rate and growth of young Atlantic menhaden. *J. Fish. Biol.* 8: 55-65.
- HILDEBRAND, H H. A study of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. *Publ. Inst. Mar. Sci. Univ. Texas* 3: 233-366.
- HILDEBRAND, H H. A study of the fauna of the pink shrimp (*Penaeus duorarum* Burkenroad) grounds in the Gulf of Campeche. *Publ. Inst. Mar. Sci. Univ. Texas* 4: 169-232.
- HOLTHUIS, L B. FAO Species Catalog Vol. 1-Shrimps and Prawns of the World. *FAO Fish. Synopsis* No. 125. 271 p.
- Hoss, D E. Energy requirements of population of pinfish *Lagodon rhomboides* (Linnaeus). *Ecology* 55: 848-855.
- HUFF, J A and COBB, S P. Penaeoid and sergestoid shrimps (Crustacea: Decapoda). Mem. Hourglass Cruises, Vol. V, Part IV. *Fla. Dept. Nat. Res., Mar. Res. Lab., St. Petersburg, Fla.* 102 p.
- IRVING, L, SCHOLANDER, P F and GRINNELL, S W. The respiration of the *Tursiops truncatus*. *J. Cell. Comp. Physiol.* 17: 145-168.
- JOHANNES, R E and SATOMI, M. Composition and nutritive value of fecal pellets of a marine crustacean. *Limnol oceanogr.* 11: 191-197.
- JOUBERT, L S and DAVIES, D H. The penaeid prawns of the St. Lucia Lake system. *So. Afr. Assoc. Mar. Biol. Res., Oceanogr. Res. Inst. Investig. Rep.* no. 13. 40 p.
- KAKUDA, S and MATSUMOTO, K. On the food habits of the white croaker *Argyrosomus argentatus*. *J. Fac. Fish. Anim. Husb. Hiroshima Univ.* 17: 133-142.
- KINCH, J C. Trophic habits of the juvenile fishes within artificial waterways—Marco Island, Florida. *Contrib. Mar. Sci.* 22: 77-90.
- KJELSON, M A, PETERS, D S, THAYER, G W and JOHNSON, G N. The general feeding ecology of postlarval fishes in the Newport River estuary. *Fish. Bull.* 73: 137-144.
- KNAPP, F T. Menhaden utilization in relation to the conservation of food and game fishes of the Texas Gulf coast. *Trans. Amer. Fish. Soc.* 79: 137-144.
- KOSADA, M. On the ecology of the penaeid shrimp, *Metapenaeopsis dalei* (Rathbun), in Sendai Bay. *J. Fac. Mar. Sci. Technol. Tokai Univ.* 10: 129-136.
- KOSAKA, M. Ecological notes on the penaeid shrimp, *Trachypenaeus curvirostris*, in Sendai Bay, Japan. *J. Fac. Mar. Sci. Technol. Tokai Univ.* 12: 167-172.
- LANE, E D. A study of the Atlantic midshipman, *Porichthys porosissimus*, in the vicinity of Port Aransas, Texas. *Contrib. Mar. Sci.* 12: 1-53.
- LEATHERWOOD, S, GILBERT, J R and CHAPMAN, D G. An evaluation of some techniques for aerial census of bottlenosed dolphins. *J. Wildl. Manage.* 423: 239-250.
- LIST, R J. Smithsonian Meteorological Tables. Sixth Revised Edition. Vol. 114. Smithsonian Collections. Smithsonian Institution Press. Washington, D. C. 527 p.
- MOFFETT, A W, MCEACHRON, L W and KEY, J G. Observations on the biology of sand seatrout (*Cynoscion arenarius*) in Galveston and Trinity Bays, Texas. *Contrib. Mar. Sci.* 22: 163-172.
- MUTHU, M S, NARASIMHAM, K A, RAO, S S, SASTRY, Y A and RAMALINGAM, P. On the commercial trawl fisheries off Kakinada during 1967-70. *Indian J. Fish.* 22: 171-186.
- NMFS (National Marine Fisheries Service). Fisheries of the United States, 1978. Current Fishery Statistics No. 7800. U S Dept. Comm. NOAA. Washington, D.C. 120 p.
- NOMURA, H and FILHO, J F. A shrimp exploratory survey in northeastern and northern Brazil, with some biological observations on *Penaeus aztecus*. *FAO Fish. Rep.* 57: 219-231.
- OGURA, N. Decomposition of dissolved organic matter derived from dead phytoplankton. p. 508-515. In: A. Y. Takenouti (ed.), Biological Oceanography of the Northern Pacific Ocean. Publ. Idemitsu Shoten (Tokyo).
- OSBOURNE, K W, MAGHAN, B W and DRUMMOND, S B. Gulf of Mexico shrimp atlas. U S Dept. Interior, Bur. Commer. Fish. Circ. No. 312. 20 p.
- OVERSHEET, R M and HEARD, R W. Food of the red drum, *Sciaenops ocellata*, from Mississippi Sound. *Gulf Res. Repts.* 6: 131-135.
- PAMATMAT, M M. Facultative anaerobeosis of benthos. p. 69-92. In: K. R. Tenore and B. C. Coull (eds.), Marine Benthic Dynamics. University of South Carolina Press, Columbia, South Carolina.
- PARKER, R H, CROWE, A L and BOHME, L S. Describe living and dead benthic (macro- and meio-) communities. Vol. I. In: W. B. Jackson and G. M. Faw (eds.), Biological/chemical survey of Texoma and Capline sector salt dome brine disposal sites off Louisiana, 1978-1979, NOAA Tech. Mem. NMFS-SEFC-25, 103 p.
- PARSONS, T R, TAKAHASHI, J and HARGRAVE, B. Biological Oceanographic Processes, Pergamon Press. New York. 103 p.
- PATELLA, F. Water surface areas within statistical subareas used in reporting Gulf coast shrimp data. *Marine Fisheries Review* 37(12): 22-24.
- PERRET, W S, BARRETT, B B, LATAPIE, W R, POLLARD, J F, MOCK, W R, ADKINS, G B, GAIDRY, W J and WHITE, C J. Cooperative Gulf of Mexico Estuarine Inventory and Study, Louisiana. Phase I, Area Description. Louisiana Dept. Wildl. Fish, 175 p.
- POWELL, A B and SCHWARTZ, F O. Food of *Paralichthys dentatus* and *P. lethostigma* (Pices: Bothidae) in North Carolina estuaries. *Estuaries* 2: 267-279.
- PRUTER, A T. Trawling results of the R/V ANTON BRUUN in the Bay of Bengal and Arabian Sea. *Commer. Fish. Rev.* 26 (11A, Suppl): 27-34.
- REID, G K, JR. An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. *Bull. Mar. Sci. Gulf Caribb.* 4: 1-94.
- REITSEMA, L A. Determine seasonal abundance, distribution, and community composition of zooplankton. Vol. II In: W. B. Jackson and G. W. Faw (eds.), Biological/chemical survey of Texoma and Capline sector salt dome brine disposal sites off Louisiana, 1978-1979. NOAA Tech. Mem. NMFS-SEFC-26, 133 p.
- RIVAS, L R. (Unpubl. report). Estimates of biomass for pelagic and coastal sharks in the Gulf of Mexico. Southeast Fisheries Center, National Marine Fisheries Service, Miami, Florida.
- ROELOFS, E W. Food studies of young sciaenid fishes, *Micropogon* and *Leiostomus*, from North Carolina. *Copeia* 1954: 151-153.
- ROGERS, R M, JR. Trophic interrelationships of selected fishes on the continental shelf of the northern Gulf of Mexico. Ph.D. Diss. Texas A and M Univ., College Station, Texas, 229 p.
- ROSS, S T. Patterns of resource partitioning in searobins (Pices: Triglidae). *Copeia* 1977: 561-571.
- ROSS, S T. Trophic ontogeny of the leopard searobin, *Prionotus scitulus* (Pices: Triglidae). *Fishery Bull.* 76: 225-234.
- RYTHER, J H. Photosynthesis and fish production in the sea. *Science* 166: 72-76.
- RYTHER, J H and GUILLARD, R R L. Studies of marine planktonic diatoms. III. Some effects of temperature on respiration of five species. *Can. J. Microbiol.* 8: 447-453.
- SACKETT, W M. In: S. Z. El-Sayed, W. M. Sackett, L. M. Jeffrey, A. O. Fredericks, R. P. Saunders, P. S. Conger, G. A. Fryxell, K. A. Steidinger, and S. A. Earle, Chemistry primary productivity, and benthic algae of the Gulf of Mexico. Folio 22, Serial Atlas of the Marine Environment. American Geographical Society, New York.
- SCHOENER, T W. Resource partitioning in ecological communities. *Science* 185: 27-39.
- SHANE, S H. Occurrence, movements, and distribution of bottlenose dolphin, *Tursiops truncatus*, in southern Texas. *Fish. Bull.* 78: 593-602.

- SHERIDAN, P F. Food habits of the bay anchovy, *Anchoa mitchilli*, in Apalachicola Bay, Florida. *Northeast Gulf Sci.* 3: 1-15.
- SHERIDAN, P F. Trophic resource utilization by three species of sciaenid fishes in a northwest Florida estuary. *Northeast Gulf Sci.* 3: 1-15.
- SHERIDAN, P F and TRIMM, D L. Summer foods of Texas coastal fishes relative to age and habitat. *Fishery Bull.* 81 (In Press).
- SIDWELL, V D. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks, and their products. *NOAA Tech. Mem. NMFS F/SEC-11*. U S Department of Commerce. Southeast Fisheries Center, Miami, Florida. 432 p.
- SIKORA, W B, HEARD, R W and DARRIGET, M D. The occurrence and food habits of two species of hake, *Urophycis regius* and *U. floridanus*, in Georgia estuaries. *Trans. Amer. Fish. Soc.* 101: 513-525.
- SKLAR, F H. Primary productivity in the Mississippi Delta bight near a shallow bay estuarine system in Louisiana. Louisiana State University, Ph.D. diss. Baton Rouge, Louisiana. 96 p.
- SPRINGER, V G and WOODBURN, K D. An ecological study of the Tampa Bay area. Fla. Dept. Nat. Res., *Mar. Res. Lab. Prof. Papers Ser.* No 1, 104 p.
- STICKNEY, R R, TAYLOR, G L, and HEARD, R W, III. Food habits of Georgia and estuaries fishes. I. Four species of flounders (Pleuronectiformes: Bothidae). *Fish. Bull.* 72: 515-525.
- STOKES, G M. Life history studies of southern flounder (*Paralichthys lethostigma*) and Gulf flounder (*P. albigutta*) in the Aransas Bay area of Texas. Texas Parks Wildl. Dept., *Tech. Ser.* No. 25. 37 p.
- STRICKLAND, J D H. Measuring the production of marine phytoplankton. *Fish. Res. Bd. Canada Bull.* 122: 172 p.
- TABB, D C and MANNING, R B. A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957 through September, 1960. *Bull. Mar. Sci. Gulf Caribb.* 11: 552-649.
- TECHNICAL CONSULTATION ON SHRIMP BY-CATCH UTILIZATION. 1982 Fish By-Catch . . . Bonus from the Sea. Report from a meeting in Georgetown, Guyana, October 27-30, 1981. 163 p.
- TIETJEN, J H. The ecology of shallow-water meiofauna in two New England estuaries. *Oecologia* 2: 251-291.
- TURNER, R E. Intertidal vegetation and commercial yields of penaeid shrimp. *Trans. Amer. Fish. Soc.* 106: 411-416.
- TYLER, A V. Food resource division among northern, marine demersal fishes. *J. Fish. Res. Bd. Canada* 29: 997-1003.
- WELSH, W W and BREDER, C M, JR. Contributions to life histories of Sciaenidae of the eastern United States coast. *Bull. U S Bur. Fish.* 39: 141-201.
- YANEZ-ARANCIBIA, A, CUIEL-GOMEZ, J and DE YANEZ, V L. 1976 Prospeccion biologica y ecologica del bagre marino *Galeichthys caeruleus* (Gunter) en el sistema lagunar costero de Guerrero, Mexico (Pisces: Ariidae), *an. Centro Cienc. Mar. Limnol. Univ. Nat. Auton. Mexico* 3 (1): 135-180.